Ocean predation and mortality of adult Atlantic salmon

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Abstract

Predation and mortality are often difficult to estimate in marine environments, which hampers the management and conservation of vulnerable fish species. Here, the ocean predation and mortality of Atlantic salmon (*Salmo salar*) were investigated across the North Atlantic Ocean, based on 156 adult Atlantic salmon tagged with pop-up satellite archival tags. Data from 22 of these fish provided evidence of predation, 37 of unknown mortality, and 58 tags detached prematurely for unknown reasons. During the ocean migration adult Atlantic salmon experienced predation from a variety of large marine animals, including toothed whales (Odontoceti), endothermic fish, and ectothermic fish. These predation events occurred primarily in waters south of Iceland and in the Gulf of St. Lawrence. Both the estimated predation rates and the total mortality rates were highest for Atlantic salmon from Canada, Ireland, and Spain, while fewer deaths were observed for Atlantic salmon from northern Europe. Of the known predation events, endothermic fish were the most common predators (n = 13). Predation by both Atlantic bluefin tuna (*Thunnus thynnus*) and porbeagle (*Lamna nasus*) occurred in the Gulf of St. Lawrence, and predation by porbeagle occurred in waters spanning from west of the Irish Shelf to the Bay of Biscay. In comparison, predation by toothed whales (n = 5) and ectothermic fish (n = 4) occurred over greater geographical areas, suggesting a lower population-specific impact imposed by these taxa. The overall geographical variation in ocean predation and mortality coincides with declines in population abundance, which are most profound for the southernmost populations.

Introduction

Predation plays a crucial role in structuring aquatic ecosystems through shifting the behaviour, distribution, and density of prey (Romare and Hansson 2003, Baum and Worm 2009, Swain et al. 2015). However, quantifying predation remains notoriously difficult, because accurate information of prey abundance is required. This is particularly the case for pelagic marine ecosystems, which cover large ocean areas and are highly dynamic in terms of species composition (Block et al. 2011, Sequeira et al. 2018).

In fisheries research, quantifying predation and mortality is of the utmost importance, due to the vulnerability of numerous populations (Hammill et al. 2014a, Chasco et al. 2017). A prime example of a species of which detailed information about predation and mortality is needed is the anadromous Atlantic salmon (*Salmo salar*). Since the early 1980s, Atlantic salmon has experienced prolonged population declines, partially due to reduced marine survival (ICES 2017). While these persistent declines have occurred throughout large parts of the species' distribution range, the negative trend is most profound for the southernmost populations (ICES 2017).

During the marine phase most Atlantic salmon migrate to oceanic areas that are distant from their river of origin, mainly utilizing pelagic habitats (Hedger et al. 2017a, Strøm et al. 2017, 2018). Knowledge about their ecology in the open ocean is primarily related to foraging (Rikardsen and Dempson 2011, Sheehan et al. 2012), with most of the information about marine mortality originating from studies carried out close to natal rivers (Cairns 2006 but see Montevecchi et al. 2002). In the ocean, Atlantic salmon constitute a minor fraction of the total prey abundance, which in combination with the incomplete knowledge about their ocean distribution, make observations of Atlantic salmon as prey a rarity even for the most important

predators (Cairns 2006). In order to derive quantitative descriptions of ocean predation and mortality, information needs to be gathered from Atlantic salmon's perspective rather than the predators', for which detailed information would not be feasible without impractically large sample sizes.

Developments in archival telemetry have facilitated a greater understanding of the ocean distribution of numerous fish species (e.g. Block et al. 2005, Righton et al. 2016, Strøm et al. 2018). In studies of the ocean migration of large pelagic fishes, the most commonly used tag type is the pop-up satellite archival tag (PSAT), which record environmental data and is programmed to detach, surface, and transmit archived data to satellites at a pre-set date (Aarestrup et al. 2009, Biais et al. 2017, Strøm et al. 2017). Premature detachment occurs if a constant depth is registered over a certain time period, or the tag records depth endangering its physical integrity. Under such circumstances, the archived data may allow inference to be made about whether or not a tagged individual has died (Stokesbury et al. 2011, Béguer-Pon et al. 2012, Lacroix 2014, Wahlberg et al. 2014, Cosgrove et al. 2015, Amilhat et al. 2016, Tolentino et al. 2017).

In contrast to Pacific salmon species (*Oncorhynchus* spp.), Atlantic salmon is iteroparous. For some populations, repeat spawners may be important contributors to population recruitment (Chaput and Jones 2006, Hubley and Gibson 2011) and it has been suggested that increased predation on this life stage may hinder the recovery of vulnerable populations (Lacroix 2014). Here, the open-ocean predation and mortality of post-spawned Atlantic salmon were investigated for fish tagged with PSATs in several rivers of the North Atlantic basin. Our aims were to 1) to quantify the mortality of PSAT tagged Atlantic salmon, 2) investigate the geographical distribution of predation events, and 3) postulate the most likely predators.

Materials and Methods

Tagging procedure

In the period 2008 – 2016, a total of 227 post-spawned Atlantic salmon were tagged with pop-up satellite archival tags (PSATs) in Canada (Miramichi and Restigouche rivers), Denmark (Skjern and Varde rivers), Ireland (Barrow, Blackwater, Nore, and Suir rivers), Norway (Alta, Neiden, and Orkla rivers), and Spain (Lérez River) (Table 1). Data from the marine migration were obtained from 156 of the tagged fish, with the remaining 71 tags failing to report data while at sea. Norwegian populations were treated as separate entities due to the geographical separation between the rivers, while data from Canadian, Danish, and Irish rivers were pooled by country due to the proximity of the study rivers. All Atlantic salmon were tagged in the spring before migrating to sea (March 14 – May 31), with date of tagging depending on location (Table 1). PSATs were deployed externally by attaching the tag to two cushioned back plates that were wired through the dorsal musculature of the fish below the dorsal fin (see Hedger et al. 2017a, Strøm et al. 2017). The body length of the tagged fish ranged from 63 – 115 cm, and the mean length of the different groups ranged from 73 cm (Ireland) to 99 cm (Alta, Norway) (Table 1).

Table 1: Overview of the number of tagged Atlantic salmon and whether the tags reported on the scheduled date, were retrieved from fish recaptured at sea or in the river as consecutive spawners, or whether they were eaten by a predator. No. endothermic fish, no. ectothermic fish, and no. marine mammals indicate the number of fish eaten by the various predator groups. Z_P indicates the predation rate and Z_M indicates the total mortality rate (including predation and unknown mortalities).

Group	No. tagged fish	Tagging period	Body length ± SD (cm)	No. reporting tags	No. reporting on scheduled date	No. marine recaptures	No. consecutive spawners	No. endothermic fish	No. ectothermic fish	No. marine mammals	No. unknown mortalities	No. unknown	Z_P	Z_M
Canada	53	Apr 20 – May 11	81 ± 8	28	6	-	2	8	1	1	5	5	1.33	2.3
Miramichi	*43*	-	-	*26*	*6*	-	*2*	*7*	*1*	*1*	*5*	*4*	-	-
Restigouche	*10*	-	-	*2*	-	-	-	*1*	-	-	-	*1*	-	-
Denmark	44	Mar 31 – Apr 8	84 ± 6	32	9	-	-	-	1	1	10	11	0.13	0.96
Skjern	*24*	-	-	*17*	*7*	-	-	-	-	*1*	*2*	*7*	-	-
Varde	*20*	-	-	*15*	*2*	-	-	-	*1*	-	*8*	*4*	-	-
Ireland	27	Mar 11 – Mar 25	74 ± 6	19	2	-	1	1	1	3	10	1	0.61	3.1
Barrow	*2*	-	-	*1*	-	-	-	-	-	-	*1*	-	-	-
Blackwater	*7*	-	-	*6*	*1*	-	*1*	-	-	-	*4*	-	-	-
Nore	*1*	-	-	*1*	-	-	-	-	-	-	*1*	-	-	-
Suir	*17*	-	-	*11*	*1*	-	-	*1*	*1*	*3*	*4*	*1*	-	-
Norway – Alta	52	May 25 – May 29	99 ± 6	41	11	4	-	-	-	-	5	21	0	0.19
Norway – Neiden	17	May 30 – May 31	92 ± 9	14	-	-	-	-	-	-	4	10	0	0.49
Norway – Orkla	20	May 5 – May 6	97 ± 6	10	4	-	-	-	-	-	1	5	0	0.19
Spain - Lerez	14	Mar 14 – Mar 18	79 ± 7	12	-	-	-	4	1	-	2	5	1.07	1.74
Total	227	Mar 14 – May 31	87 ± 11	156	32	4	3	13	4	5	37	58	-	-

Tag details

The PSATs (X-tag, Microwave Telemetry, Inc.) were 120 mm long (273 mm including the antenna), had a diameter of 32 mm, weighed 40 g in air, were slightly buoyant, and had a lifespan of 16 months. Tags were programmed to release after 112 – 312 days, if the pressure was constant for 3 – 5 days, or if the pressure sensor recorded depths endangering its physical integrity (manufacturer specified at 1250 m). During deployment, X-tags recorded temperature, depth, and light intensity at two-minute intervals. The complete data set was only available if tags were retrieved. Transmitted data only contained a subset of the archived information because of limited battery life and connection to the Argos satellite system. The temporal resolution of the transmitted depth and temperature data depended on the deployment period, whereas for the light-based data only estimated sunrise and sunset times and daily geolocation estimates were transmitted. The X-tag implemented data compression techniques prior to transmission, which could cause tags to report distorted temperature and depth values flagged as delta limited. These delta-limited values were present if the rate of change exceeded a certain threshold. This causes overestimation of variables during rapid decrease and underestimation of variables during rapid increase (http://www. microwavetelemetry.com).

Quantifying predation events and mortalities

Premature tag detachment occurred due to predation, unknown mortalities, and for unknown reasons. For tags detaching prematurely, tag data were investigated to identify the fate of the tagged fish. Tag consumption was recognised by the tag failing to record light during periods when daylight should have been detected, in combination with simultaneous observations of vertical movements. For these tags, the vertical profile around the period of mortality was scrutinized to identify whether the tagged Atlantic salmon was eaten alive or scavenged after its death (Figure 1). Scavenging was determined when the tag recorded a steady descent through

the water column, indicating that the Atlantic salmon had died before the tag was ingested (Figure 1). Predation was inferred when this pattern was absent (Figure 1). For Atlantic salmon identified as eaten by predators, temperature profiles during ingestion were further investigated (Figure 1). If the temperature increased above the ambient water temperature, predation by an endotherm was inferred. Tags recording temperatures of approximately 37 ℃ were classified as ingested by marine mammals, whereas tags with temperatures not reaching this level were classified as eaten by endothermic fish. If there was no abrupt increase in temperature after ingestion, predation by an ectotherm was inferred.
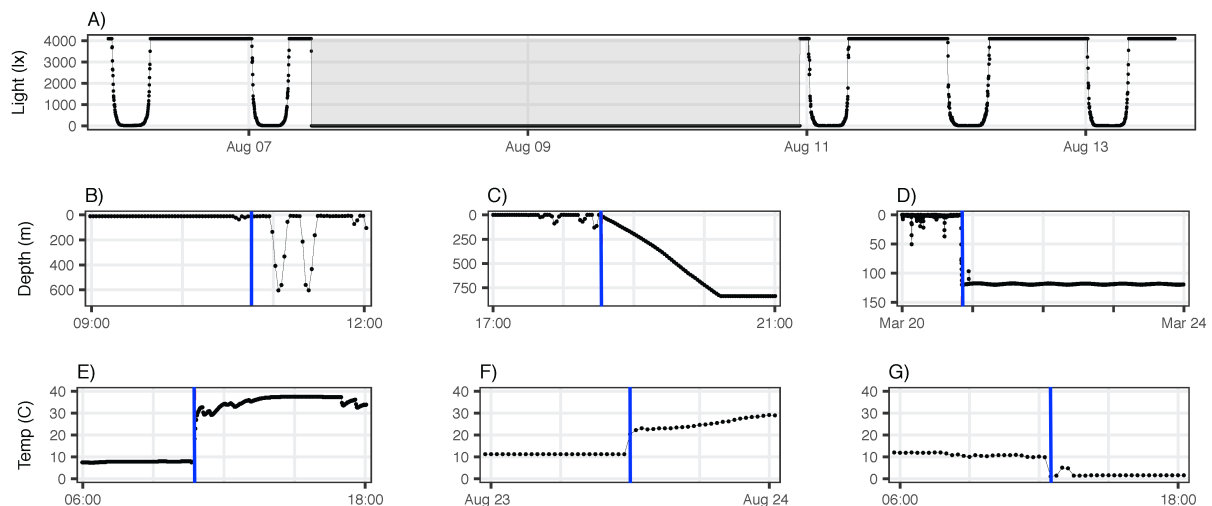
Figure 1: A) Light profile for a retrieved tag around the period of ingestion, with grey area indicating time inside the predator. B) Depth profile of a consumed Atlantic salmon. C) Depth profile of an Atlantic salmon dying at the surface that was later scavenged. D) Depth profile of an Atlantic salmon carcass sinking to the ocean floor. Temperature profiles of an Atlantic salmon consumed by a marine mammal (E), an endothermic fish (F), and an ectothermic fish (G). Blue vertical lines indicate estimated time of mortality.

For tags reporting prematurely with no evidence of ingestion, tag data were inspected to determine if there were clear signs that the fish had died or not. Tags transmitting data after a period on the ocean floor and tags that recorded a steady descent before triggering the pressure

fail-safe mechanism were, in addition to the scavenged tags, indicating fish mortality. The reasoning behind this is that the inherent buoyancy of the tags implies that sinking tags were attached to parts of an Atlantic salmon carcass (Figure 1). In contrast, tags reporting prematurely after floating at the surface were considered to detach for unknown reasons. In order to obtain a conservative measurement of predation and total mortality rates, these fish were considered alive until tag detachment, because they could be live fish that had lost their tag, either due to attachment failure or due to the fish cruising at the surface for a prolonged period, triggering the tag's release mechanism. The total mortality in each group included fish experiencing unknown mortalities and predation. Group-specific instantaneous predation (Z_P) and total mortality (Z_M) rates were calculated following Ricker (1975):

$Z_P = [- \ln(N_P/N_I)] / t$

$Z_M = [- \ln(N_M/N_I)] / t$

where N_P/N_I is the proportion of the sample that did not experience predation, N_M/N_I is the proportion of the sample not experiencing unknown mortality or predation, and t is the mean deployment duration given as the fraction of one year. The difference in length between fish that died and fish that were alive throughout the pre-programmed deployment period was investigated independently for the groups using permutation tests. Alive fish included individuals with tags detaching at the pre-programmed date, whereas dead fish included premature detachment either due to predation or mortality. Only groups with several fish alive throughout the deployment period and several confirmed mortalities were tested.

Predator identification

The method of predator identification varied depending on predator type and geographical

location of the predation event. For tags ingested by marine mammals, ectotherms, and endothermic fish in the northeast Atlantic Ocean, predators were postulated by first identifying the potential predators of sufficient size with a spatial distribution overlapping the predation events. This was followed by a visual comparison of the recorded data during the ingestion period against behavioural data obtained from the literature for the candidate predators. For the Atlantic salmon ingested by marine mammals, the general tendency of pinnipeds, orcas (*Orcinus orca*), and other oceanic dolphins (Delphinidae) to tear apart large salmonids at the surface (Roffe and Mate 1984, Middlemas et al. 2003, Vester and Hammerschmidt 2013), implies that these fish were consumed by other marine mammals, because these foraging strategy would likely not lead to tag ingestion. For the remaining predation events, the candidate predators encompassed large pelagic and benthic fish for the Atlantic salmon eaten by ectotherms, and lamnid sharks (Lamnidae) and Atlantic bluefin tuna (*Thunnus thynnus*) for the individuals ingested by endothermic fish in the northeast Atlantic Ocean.

For Atlantic salmon consumed by endothermic fish in the northwest Atlantic Ocean, predation by either Atlantic bluefin tuna or porbeagle (*Lamna nasus*) was assumed *a priori*, because these are the only warm-gutted fish frequently occupying waters overlapping the observed predation events. The most likely predators were identified by a linear discriminant analysis (LDA) because data on the vertical behaviour of both Atlantic bluefin tuna and porbeagle were available from waters in proximity to the predation events (Campana et al. 2010, Stokesbury et al. 2011). The LDA identifies the linear combination of variables that creates the greatest between-group variance for objects with known affiliation, which in a subsequent step can be used to predict the affinity of unknown entities. This method has previously been used for identifying the most likely predators of American eel (*Anquilla rostrata*) tagged with PSATs (Béguer-Pon et al. 2012).

LDA variables were derived from the vertical time series of four Atlantic bluefin tuna tagged in the Gulf of St. Lawrence in the autumn (Stokesbury et al. 2011) and from two porbeagle tagged off eastern Canada during the summer (Campana et al. 2010) (Table 2, Supplementary figure 1). As these reference data sets consisted of physically recovered tags with a higher temporal resolution than the consumed tags, the reference time series were sub sampled to match the resolution of the consumed tags (Table 2). The input variables in the LDA were selected based on their discriminating ability and included percentage of time spent in the upper 20 m of the water column (% surface), the difference in maximum depth between day and night (diel amplitude), and the 95 percentiles of the depth recordings (95%) (Table 2).

For the Atlantic bluefin tuna, only data from the period when the fish were resident in the Gulf of St. Lawrence were included in the reference data set (Table 2). For the porbeagle, data until November 1 were used (Table 2). To correct for post-release behaviour (Hoolihan et al. 2011), the initial period following tagging was investigated for all reference tags. If a modified behaviour was detected shortly after tagging, days including this behaviour were omitted from the analysis.

Table 2: Data obtained from the tagged Atlantic salmon (AS) consumed by endothermic fish in the northwest Atlantic Ocean and data from the endothermic predators used in the linear discriminant analysis (ABFT = Atlantic bluefin tuna, PB = porbeagle). Duration indicates the time at liberty for the Atlantic salmon (AS) and the length of the time series for the predators (ABFT and PB). Resolution indicates the temporal resolution of the tag data. Date indicates the time of predation for the Atlantic salmon (AS) and start of time series for the predators (ABFT and PB). % surf is the proportion of time spent near the surface (< 20 m), diel amplitude is the difference in maximum depth between day and night, and 95% is the 95-percentile depth. T_{Max} is the maximum stomach temperature of the predator, T_E is the thermal excess, and T_D is the maximum difference in stomach temperature of the predator.

	Tag ID	Duration (d)	Resolution (Δt)	Date	% surf	Diel amplitude (m)	95% (m)	Max depth (m)	T_{Max} (°C)	T_E (°C)	T_D (°C)	Most likely predator
AS	117454	46	15 min	17/6/12	66	43	32	135	26.9	17.9	9.9	ABFT
AS	117458	35	15 min	20/6/12	92	35	25	97	25.1	16.3	6.5	ABFT
AS	117463	24	15 min	8/6/12	99	6	14	22	21.9	11.5	7.4	ABFT
AS	128019	23	2 min	5/6/13	89	15	29	73	26.7	17.2	10.7	ABFT
AS	128023	34	15 min	30/6/13	72	161	123	215	26.9	13.7	5.5	PB
AS	136019	36	15 min	2/7/14	69	86	156	182	26.2	14.5	6.3	PB
AS	148256	79	15 min	1/8/15	96	312	14	355	24.1	16.3	8.3	-
AS	158494	25	15 min	25/6/16	35	116	48	188	26.5	17.4	9.7	PB
ABFT	100864	18	30 s	11/9//10	87	0	25	-	-	-	-	-
ABFT	100905	34	30 s	1/9/10	98	6	16	-	-	-	-	-
ABFT	100906	25	30 s	1/9/10	94	-1	21	-	-	-	-	-
ABT	100913	14	30 s	12/9/10	70	2	28	-	-	-	-	-
PB	07A0946	96	10 s	16/7/08	45	40	196	-	-	-	-	-
PB	07A0946	13	10 s	19/10/08	19	-12	118	-	-	-	-	-
PB	08A0999	44	10 s	14/8/10	17	41	38	-	-	-	-	-
PB	08A0999	29	10 s	26/9/10	15	0	87	-	-	-	-	-

As both porbeagle used for predator reference displayed distinct vertical movement patterns, a split-moving window analysis was conducted in order to objectively separate different behavioural modes (Humphries et al. 2010). The analysis was initiated by constructing a time-at-depth matrix, using the proportion of time spent in 25 m depth bins (rows) during all 12 h periods (columns) in the time series. A virtual window, with a width of four time bins, was then placed at the start of the time series and the Euclidean distance between the two window halves was calculated. The calculated dissimilarity was assigned to the centre of the window, and the window progressed through the time series. This process was repeated for window widths from 4 to 20, stacking the dissimilarity values vertically (Supplementary figure 2). The statistical significance of the dissimilarities was calculated using a permutation technique that reshuffled the time-at-depth matrix 1000 times (Humphries et al. 2010). The number of times the permuted dissimilarities exceeded the true dissimilarity at that position was then counted and converted into a p-value. P-values were stacked vertically and significant changes in vertical behaviour were identified (Supplementary figure 2). The discrete behavioural modes generated by this analysis were treated as independent entities in our analysis (Table 2).

Results

Overview of tag with premature reports

Of the 156 reporting tags, 32 tags reported on the scheduled date, 3 tags were retrieved from consecutive spawners that returned to the river after spending the summer at sea, and 4 fish were recaptured in marine fisheries (Table 1). These 39 fish were confirmed alive throughout the deployment period. The remaining 117 tags detached prematurely, with 22 tags providing evidence of marine predation, 37 detaching due to unknown marine mortality, and 58 for unknown reasons (Table 1). Unknown mortalities included 33 tags that transmitted data after a

period at the ocean floor, 3 tags that recorded depths exceeding the pre-set threshold, and 1 tag that was scavenged. The percentage of reporting tags detaching prematurely for unknown reasons, varied between 5 – 71% for the different groups and was highest for the Norwegian populations (50 – 71%).

Predation was inferred for fish from Canada, Denmark, Ireland, and Spain (Table 1, Figure 2). No predation was recorded for the Norwegian populations (Table 1), despite that the Norwegian Atlantic salmon comprised 42% of the reporting tags. The estimated instantaneous predation rates were 1.33 Yr^{-1} for the Canadian fish; 1.07 Yr^{-1} for the Spanish fish; 0.61 Yr^{-1} for the Irish fish; 0.13 Yr^{-1} for the Danish fish; and 0 Yr^{-1} for fish from Alta, Neiden, and Orkla (Table 1, Figure 3). Predation percentages varied between 0 and 42% for the different groups.
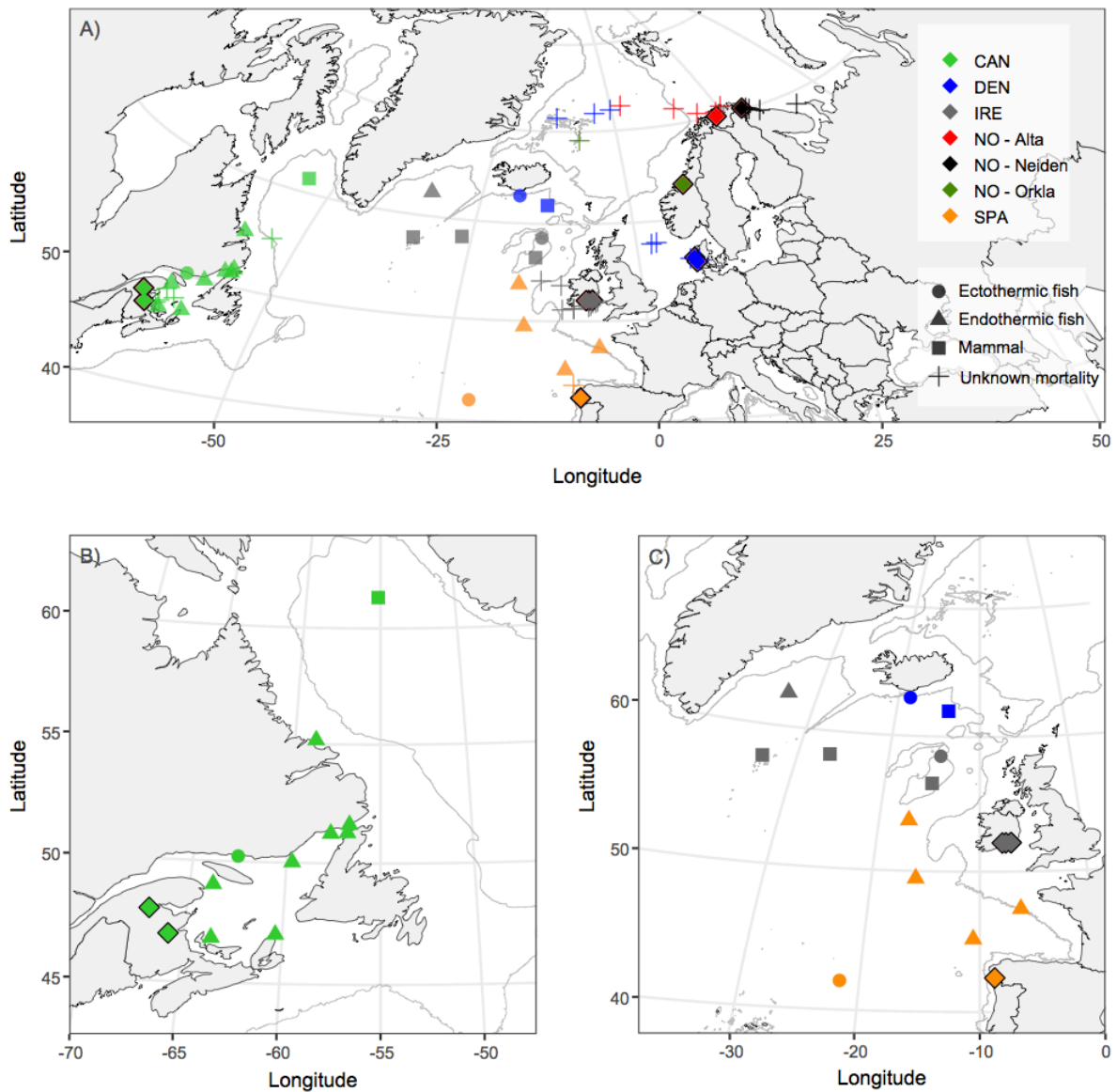
Figure 2: Pop-up locations for the tags surfacing due to assumed fish mortality (A), and pop-up locations for the tags ingested by predators in the northwest (B) and northeast Atlantic Ocean (C). Grey lines indicate the 1000 m bathymetry contour. Symbol shapes indicate cause of mortality and colours indicate the country of origin. Diamonds indicate river locations.

Unknown mortalities occurred in all groups. The estimated total morality rates (predation and unknown mortalities combined) were: 3.1 Yr^{-1} for the Irish fish, 2.3 Yr^{-1} for the Canadian fish, 1.74 Yr^{-1} for the Spanish fish, 0.96 Yr^{-1} for the Danish fish, 0.49 Yr^{-1} for the Neiden fish, 0.19 Yr^{-1} for the Alta fish, and 0.19 Yr^{-1} for the Orkla fish (Table 1, Figure 3). Group-specific total

mortalities ranged from 10 – 79%. Unknown mortalities primarily occurred in coastal waters off continental Europe close to the tagging locations, along the southern coast of Ireland, in the Gulf of. St Lawrence, and in oceanic waters in proximity to the Jan Mayen Island (Figure 2). No size difference was detected between dead and alive fish for the populations with several mortalities and several individuals confirmed alive until tag detachment (Alta, Canada, and Denmark) (permutation test; p-values 0.12 – 0.79).
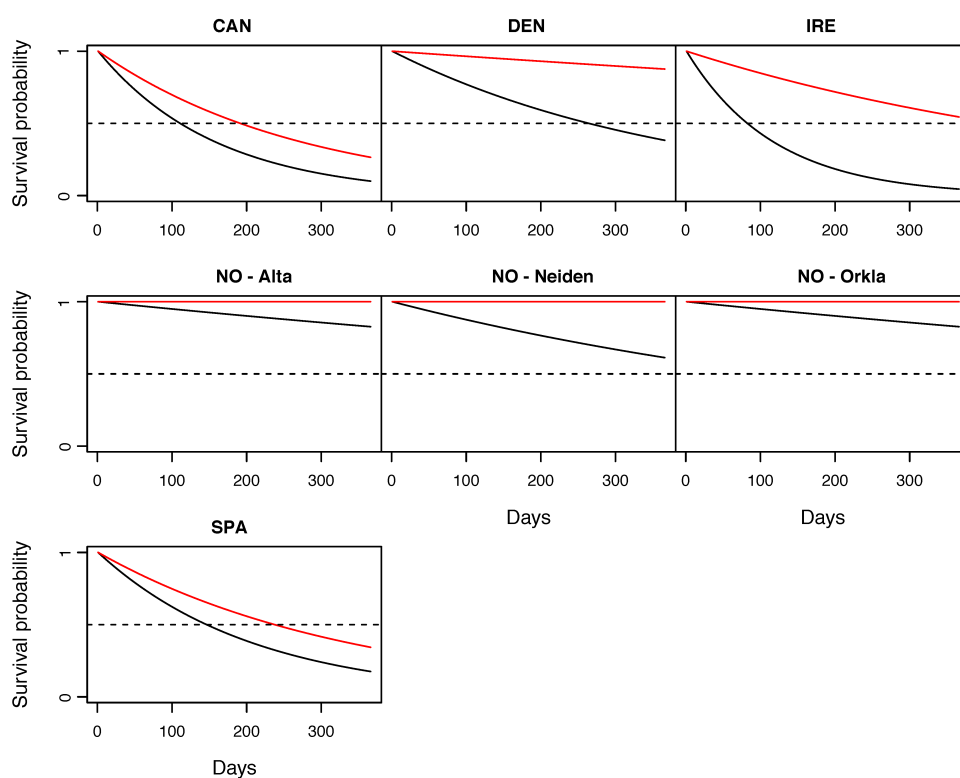
Figure 3: Annual survival probability for all Atlantic salmon groups. Black lines are the survival probability according to the total mortality rate, whereas red lines are deaths due to known predation events. Stippled horizontal lines indicate 50% annual mortality.

Predation by mammals

Five Atlantic salmon were eaten by marine mammals (Table 3). These fish originated from Canada (n = 1), Denmark (n = 1), and Ireland (n = 3), and were consumed in the period from May 9 to August 7. All four tags attached to European Atlantic salmon surfaced in waters south

of Iceland, whereas the tag attached to the Canadian Atlantic salmon surfaced in the Labrador Sea (Figure 4). During ingestion, the maximum depth ranged from 215 – 818 m (mean = 577 m, SD = 240 m) (Table 3), with frequent diving to below 400 m depth registered for three tags (Figure 4, Supplementary figure 3). The tags consumed south of Iceland, were ingested for 5 – 21 h, while the tag consumed in the Labrador Sea was ingested for 84 h (Figure 4, Supplementary figure 3).

Table 3: Data from tags consumed by marine mammal and ectothermic fish. Duration indicates the time at liberty for the Atlantic salmon. Resolution indicates the temporal resolution of the tag data.

Atlantic salmon			Predation events			
Tag ID	Groups	Duration (d)	Resolution (min), Δt	Date of predation	Max depth (m)	Most likely predator
148263	Canada	61	2	7/8/15	762	Toothed whale
34866	Ireland	52	15	9/5/11	215	Toothed whale
34877	Ireland	63	15	27/5/10	599	Toothed whale
35086	Ireland	74	15	7/6/10	491	Toothed whale
115242	Denmark	42	15	14/5/12	818	Toothed whale
117461	Canada	39	15	29/6/12	172	Ectotherm
136052	Denmark	99	15	12/6/14	780	Ectotherm
34460	Ireland	76	15	2/6/11	915	Ectotherm
136037	Spain	11	15	29/3/14	414	Swordfish
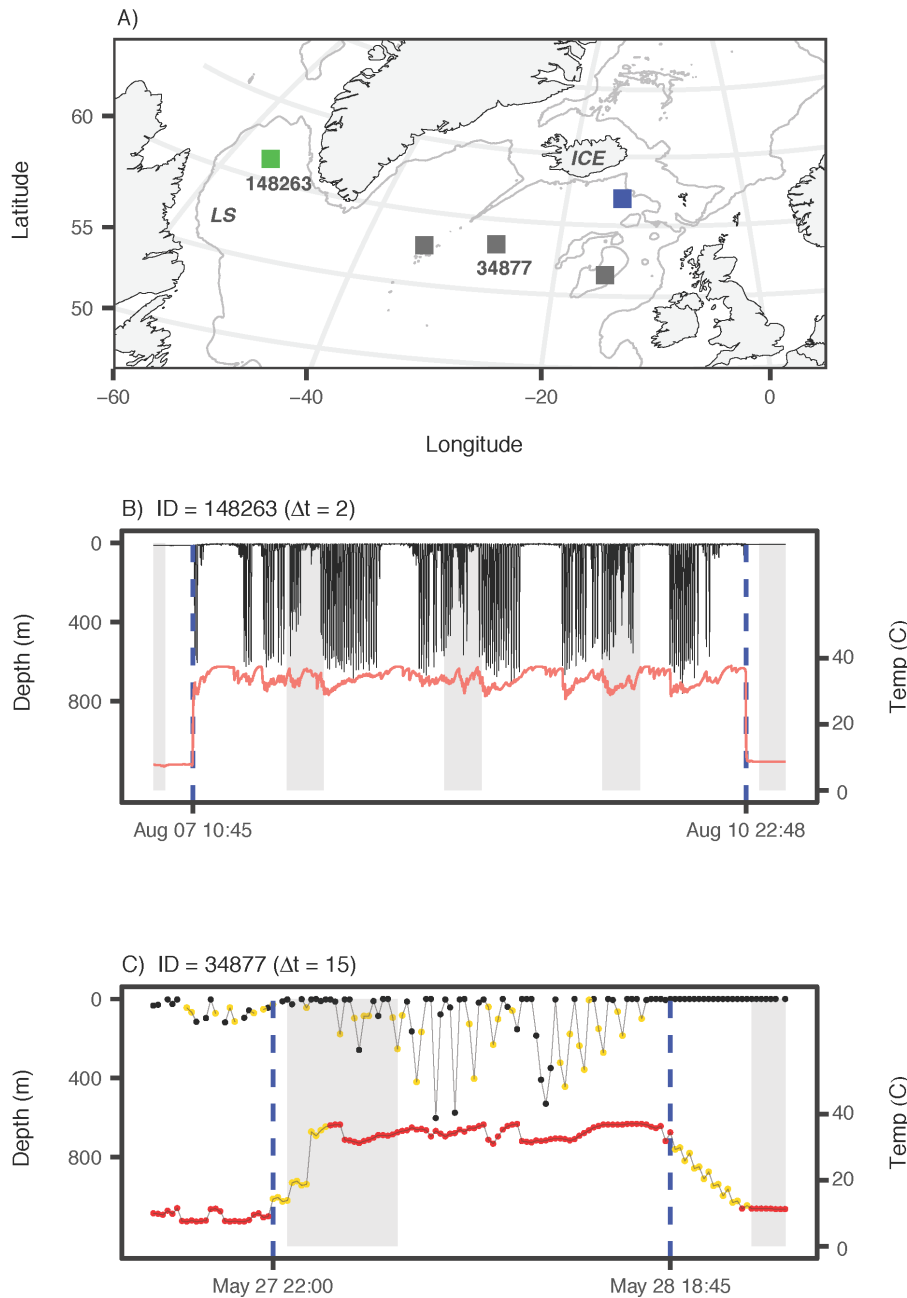
Figure 4: A) Pop-up locations for the tags consumed by marine mammals (*ICE* = Iceland and *LS* = Labrador Sea). Grey lines indicate the 1000 m bathymetry contour. B) Depth (black) and temperature (red) profile for the retrieved tag consumed in the Labrador Sea. C) Depth and temperature profile for one tag that was ingested in the northeast Atlantic Ocean. Black points indicate true depth recordings, red points indicate true temperature values, and yellow points indicate distorted values (delta-limited values). Blue vertical lines indicate time of consumption and expulsion. Shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panels.

The tag consumed by a marine mammal in the Labrador Sea was successfully retrieved and therefore facilitated a more detailed investigation. During the 84 h ingestion period, 320 dives were identified. These dives ranged in duration from 4 – 18 min (SD = 4 min) and in maximum depth from 10 – 761 m (SD = 270). Both the duration and maximum depth of the dives had a bimodal distribution (Figure 5). The archived data revealed substantial fluctuations in temperatures, primarily associated with diving, and the lowest temperature recorded was 27.6 °C (Figure 4).
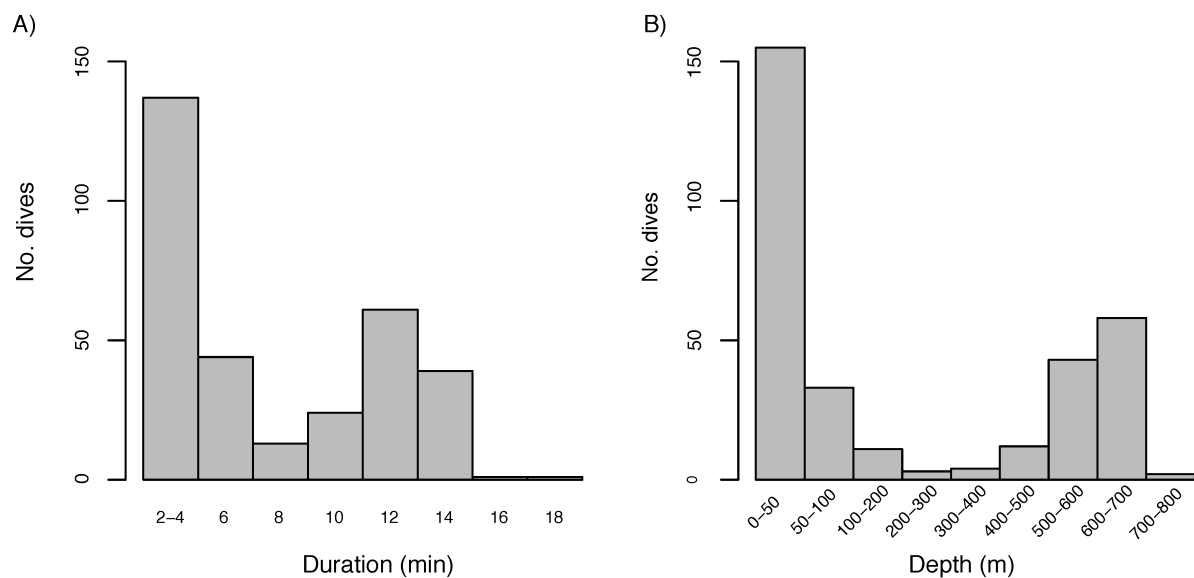
Figure 5: Counts of the duration (A) and maximum depth (B) of dives (n = 320) recorded by the retrieved tag (ID = 148263) attached to an Atlantic salmon consumed by a marine mammal in the Labrador Sea.

Predation by ectothermic fish

Predation by ectothermic fish occurred across the Atlantic Ocean and included Atlantic salmon from Canada (n = 1), Denmark (n = 1), Ireland (n = 1), and Spain (n = 1) (Table 3). Three predators displayed a non-surface-oriented behaviour (Figure 6, Supplementary figure 4), whereas one predator spent 61% of its time in the upper 20 m of the water column (Figure 7). Overall, maximum depth ranged from 172 – 915 m (mean = 570 m, SD = 339) (Table 3).

Pop-up locations for the tags consumed by deep-dwelling predators were in the Gulf of St. Lawrence and in waters south of Iceland (Figure 6). These predation events occurred from June 2 to June 29. The depth profiles during ingestion indicated large variation in depth use, with the difference between minimum and maximum depth ranging from 98 – 422 m (Figure 6, Supplementary figure 4).
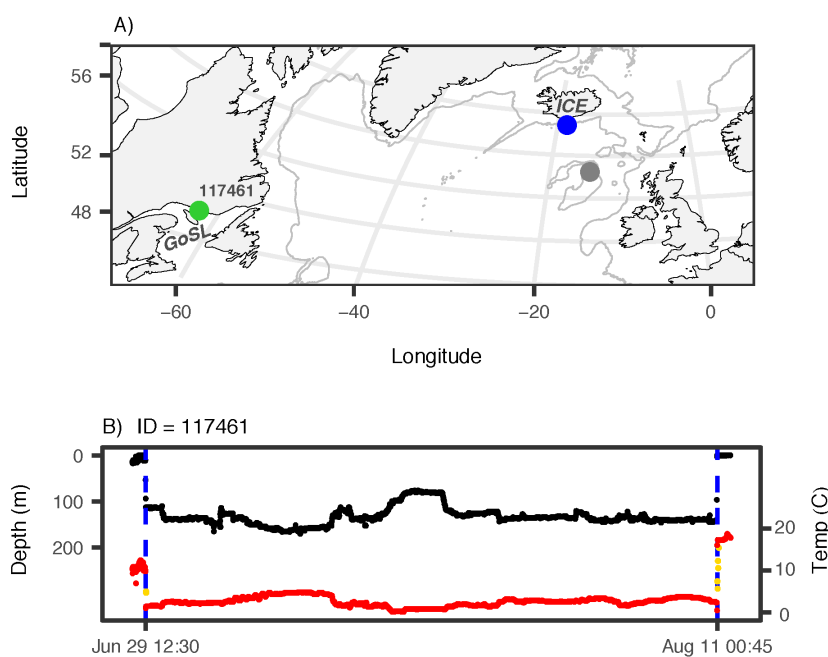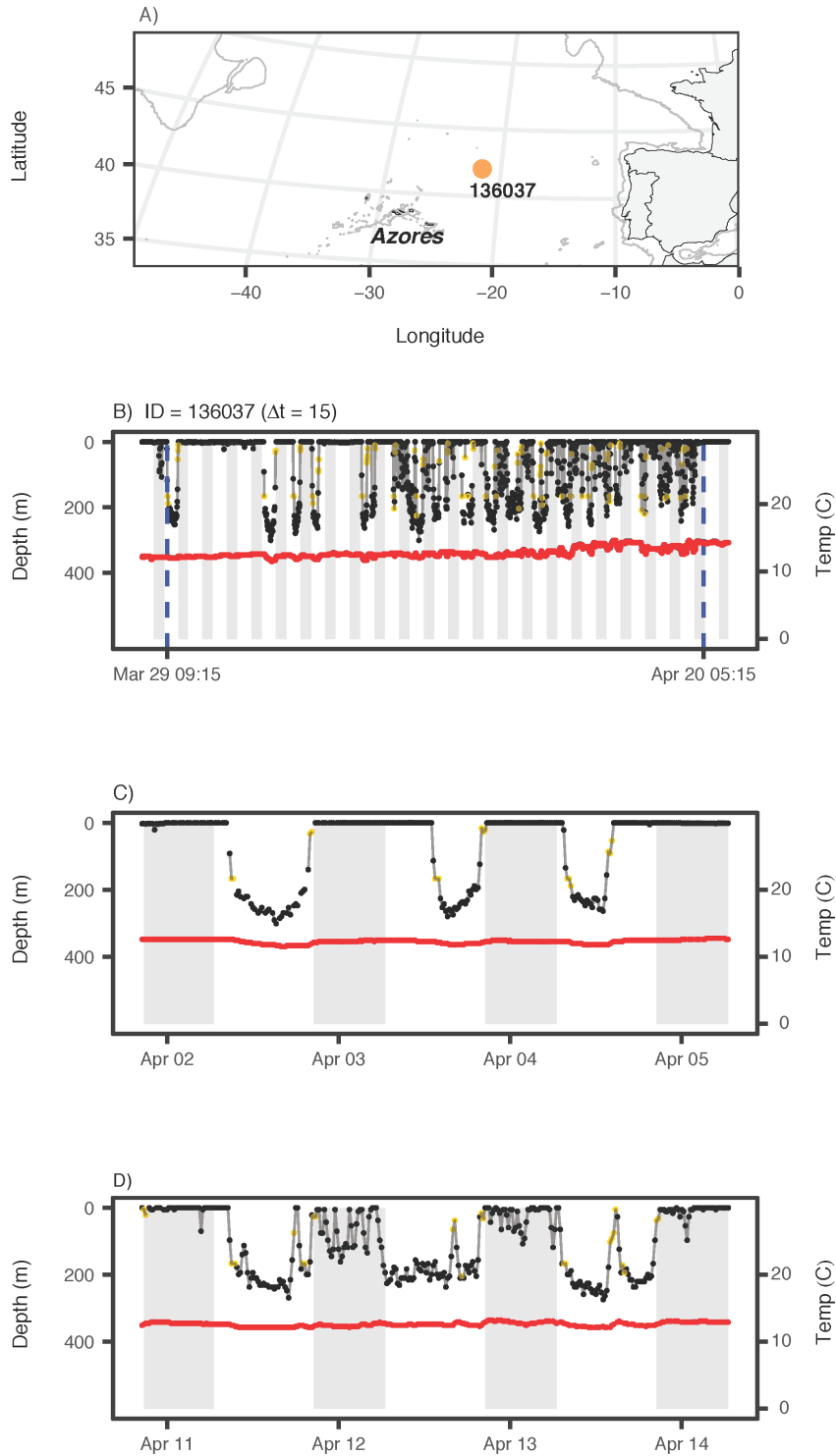

Figure 6: A) Pop-up locations of the tags consumed by deep-dwelling ectothermic fish, with grey lines indicating the 1000 m bathymetry contour (*GoSL* = Gulf of St. Lawrence and *ICE* = Iceland). B) Depth (black points) and temperature (red points) profile for a tag ingested in the Gulf of St. Lawrence. Yellow points indicate distorted values (delta-limited values) and blue vertical lines indicate time of consumption and expulsion. Tag ID is given above panel B.

Figure 7: A) Pop-up location for the tag consumed by a pelagic ectothermic fish, with grey lines indicating the 1000 m bathymetry contour. B) The depth (black points) and temperature (red points) profile during the entire ingestion period, with blue vertical lines indicating the time of consumption and expulsion. C – D) Examples of different dives displayed by the predator. Yellow points indicate distorted values (delta-limited values), and shaded regions indicate night (tag ID and temporal resolution of time series data, Δt, are stated above panel B).

The tag consumed by a pelagic ectothermic fish was ingested on March 29 and surfaced north of the Azores (Figure 7). The vertical profile depicted regular dives to depths exceeding 200 m (Figure 7). These dives were either continuous throughout most of the daylight period or disrupted by short surfacing (i.e. basking) events (Figure 7). Greater depths were utilized during the day than at night (Figure 7) (permutation test; p-value < 0.01). Vertical movements were confined to the mixed layer, with temperature recordings ranging from 11.5 – 14.6 ºC (Figure 7).

Predation by endothermic fish

Predation by endothermic fish was evident for Atlantic salmon from Canada (n = 8), Ireland (n = 1), and Spain (n = 4) (Table 2 and 4).

Table 4: Data from the tags consumed by endothermic fish in the northeast Atlantic Ocean. Duration indicates the time at liberty for the Atlantic salmon. Resolution indicates the temporal resolution of the tag data. % surf is time spend at depths < 20 m, T_{Max} is the maximum stomach temperature of the predator, T_E is the thermal excess, and T_D is the maximum difference in stomach temperature of the predator.

Atlantic salmon				Predation events						
ID	Group	Duration (d)	Resolution (min), Δt	Date of predation	Max depth (m)	% surf	T_{Max} (°C)	T_E (°C)	T_D (°C)	Most likely predator
34867	IRE	158	30	23/8/11	11	100	29.1	18.6	8.8	-
127792	SPA	18	15	1/4/13	737	55	27.8	16.9	9.2	Porbeagle
127793	SPA	24	15	7/4/13	260	85	25.0	13.4	9.9	Porbeagle
128004	SPA	7	15	21/3/13	204	98	23.6	11.8	4.8	Porbeagle
136038	SPA	7	15	25/3/14	565	49	26.9	14.6	9.4	Porbeagle

1. Northwest Atlantic Ocean

For the eight tags consumed by endothermic fish in the northwest Atlantic Ocean, predation events occurred between June 5 and August 1 (Table 2). Seven of the eight predation events occurred in the Gulf of St. Lawrence and one occurred at the Labrador Shelf (Figure 8). Only tags consumed in the Gulf of St. Lawrence were included in the linear discriminant analysis (LDA). The degree of surface orientation varied among the predators, with time spent in the upper 20 m of the water column ranging from 35 to 99% (Table 2). The maximum depth ranged from 22 – 355 m (mean = 158 m, SD = 103 m) (Table 2, Figure 8, Supplementary figure 5).
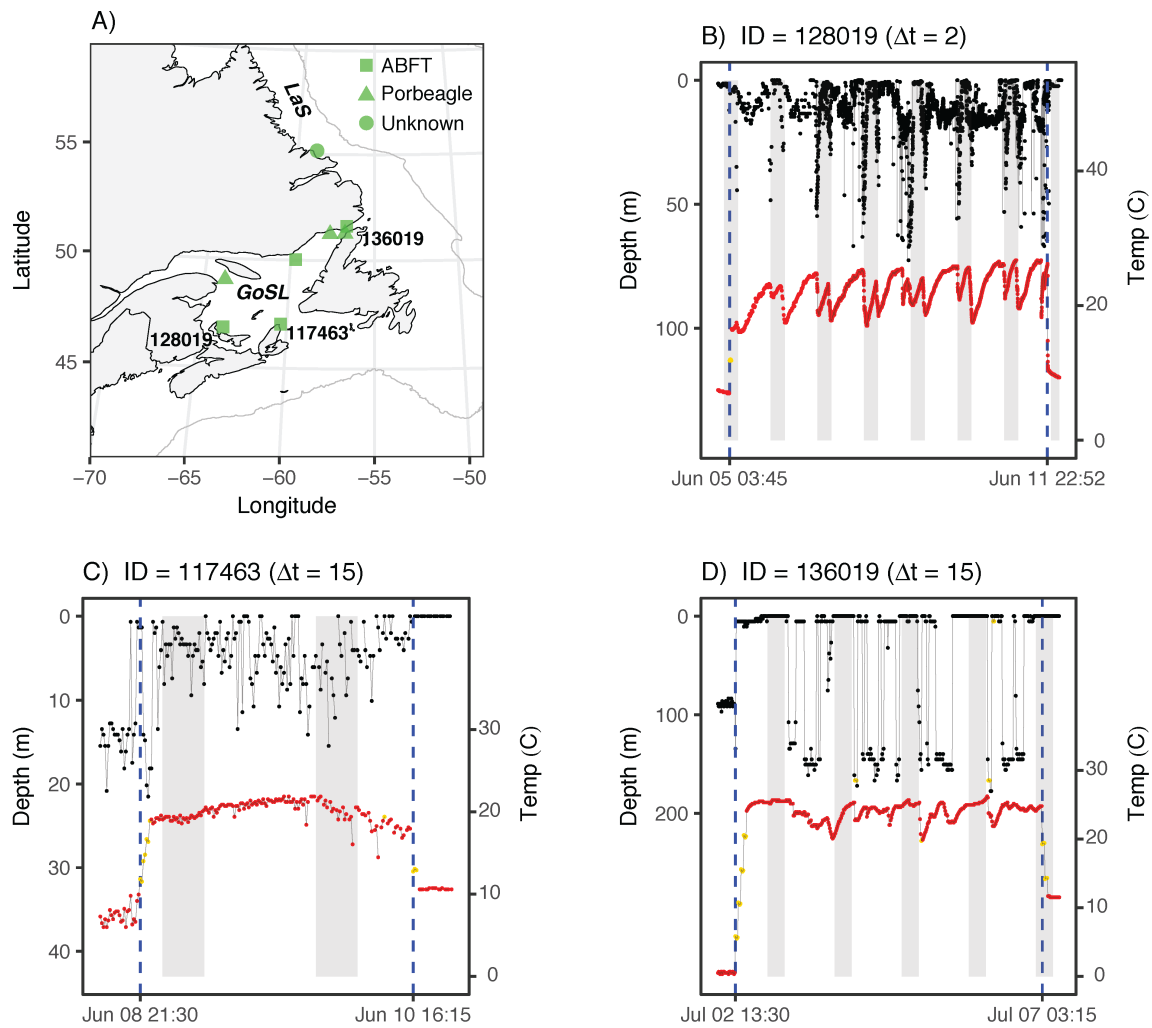
Figure 8: A) Pop-up locations for the Atlantic salmon consumed by endothermic fish in the northwest Atlantic Ocean (*GoSL* = Gulf of St. Lawrence and *LaS* = Labrador Shelf), coded by the most likely predator according to the linear discriminant analysis. Grey lines indicate the 1000 m bathymetry contour. B – C) Depth (black points) and temperature (red points) profiles for two Atlantic salmon eaten by Atlantic bluefin tuna. D) Example of the depth (black points) and temperature (red points) profile for an Atlantic salmon eaten by a porbeagle. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion, and shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panels.

For the reference data from Atlantic bluefin tuna and porbeagle, the LDA successfully separated the two species based on the three selected variables (Table 2). Based on the reference data, Atlantic bluefin tuna spent more time in surface waters compared to the porbeagle, which utilized deeper waters and displayed greater diel amplitudes when in certain behavioural modes

(Table 2). According to the LDA, Atlantic bluefin tuna was the most likely predator in four of the seven predation events in the Gulf of St. Lawrence (Table 2).

The maximum gut temperature (T_{Max}) ranged from 21.9 – 26.9 ℃ for the tags predicted to be consumed by Atlantic bluefin tuna and from 26.2 – 26.9 ℃ for the tags predicted to be consumed by porbeagle (Table 2). For the tag ingested over the Labrador Shelf, T_{Max} was 24.1 ℃ (Table 2). The difference between the maximum gut temperature and the mean ambient water temperature after surfacing (T_E) ranged from 11.5 – 17.9 ℃ for tags consumed by Atlantic bluefin tuna and from 13.7 – 17.4 ℃ for those consumed by porbeagle (Table 2). For the tag consumed over the Labrador Shelf, T_E was 16.3 ℃ (Table 2). All predators displayed variation in stomach temperatures and the difference between the maximum and the minimum temperature during ingestion (T_D) ranged from 5.5 to 10.7 ℃ (Table 2).

2. Northeast Atlantic Ocean

All of the Spanish fish eaten by endothermic fish (n = 4) were consumed prior to April 7 in waters spanning from west of the Irish Shelf to the Bay of Biscay (Figure 9). The Irish Atlantic salmon that was eaten by an endothermic fish, was consumed on August 23 in the Irminger Sea (Figure 9). Overall, the endothermic fish spent 49 – 100% of their time in surface waters (depths < 20 m) and the maximum depth ranged from 11 – 737 m (mean = 363 m, SD = 289 m) (Table 4, Figure 9, Supplementary figure 6). T_{Max} values of predators ranged from 23.6 – 29.1 ℃ and T_E from 11.8 – 18.6 ℃ (Table 4). Variation in stomach temperatures was recorded by all tags, with T_D ranging from 4.8 – 9.9 ℃ (Table 4).
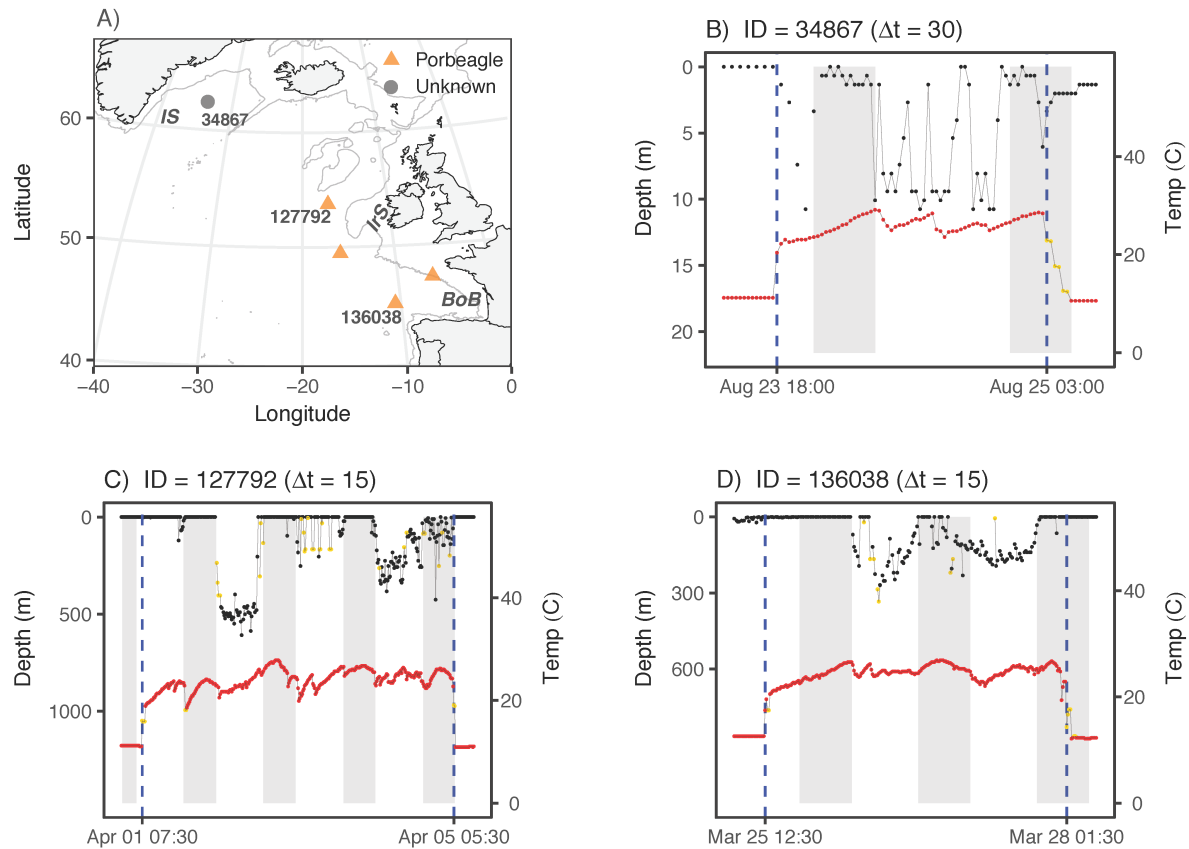
Figure 9: A) Pop-up locations for the Atlantic salmon consumed by endothermic fish in the northeast Atlantic Ocean (*BoB* = Bay of Biscay, *IrS* = Irish Shelf, and *IS* = Irminger Sea), coded by the most likely predator. Grey lines indicate the 1000 m bathymetry contour. B) Examples of the depth (black points) and temperature (red points) profile for an Atlantic salmon eaten an unknown endothermic fish. C – D) Examples of the depth (black points) and temperature (red points) profiles for two Atlantic salmon eaten by porbeagle. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion, and shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panel.

Discussion

This study is the first to describe ocean predation and mortality of adult Atlantic salmon over large parts of the species' distribution range, documenting how ocean mortality may vary between different geographical areas. This study provides direct evidence that Atlantic salmon were eaten by various marine predators during their ocean migration, including predation from

marine mammals, endothermic fish, and ectothermic fish. In addition, several unknown mortalities were observed.

While marine mammals have previously been recorded feeding on Atlantic salmon (Middlemas et al. 2003, Vester and Hammerschmidt 2013), this study is the first to record mammal predation on PSAT tagged individuals. By investigating the depth use of the mammals during the ingestion periods, large toothed whales (Odontoceti) were considered the predators. However, identifying the most likely predator species was difficult because the recovered data were either distorted by the X-tags' compression technique or of insufficient temporal resolution for comparison with behavioural data from diving whales. In the northeast Atlantic Ocean, the potential predators were the long-finned pilot whale (*Globicephala melas*) and the sperm whale (*Physeter macrocephalus*), because these are the only deep-diving whales occurring in waters overlapping the predation events. For the Atlantic salmon consumed in the Labrador Sea, the potential predators were the beluga whale (*Delpinapterus leucas*) and the long-finned pilot whale, because their diving behaviour corresponds well with the retrieved data (Heide-Jørgensen et al. 2002, Citta et al. 2013) and dives in sperm whales last substantially longer (Watwood et al. 2006, Irvine et al. 2017). Notably, the tag consumed in the Labrador Sea was retained inside the predator for a longer period than tags ingested by marine mammals in the northeast Atlantic Ocean. This might suggest that the tag was stuck in the predator's intestine and therefore that it had been eaten by a smaller whale. As adult sperm whales are of substantially larger size than long-finned pilot whales and beluga whales, sperm whales may be the most probable predator for the predation events south of Iceland, because the shorter ingestion periods may indicate that they were eaten by a large whale where a tag could rapidly pass through the intestine.

Our study is the first to provide evidence of predation on PSAT tagged adult Atlantic salmon by deep-dwelling endothermic fish. However, as little is known about the spatial distribution and vertical behaviour of large deep-dwelling fish, identifying the most likely predators was therefore considered too speculative. In comparison, predation by a pelagic ectothermic fish has previously been observed for PSAT tagged Atlantic salmon (Lacroix 2014). For the individual consumed north of the Azores, the predator's depth use, with long lasting day-time dives, resembled vertical behaviours known from blue sharks (*Prinoace glauca*) (Campana et al. 2011, Howey et al. 2017) and swordfish (*Xiphias gladius*) (Sepulveda et al. 2010, Dewar et al. 2011). For blue sharks, the vertical behaviour vary depending on time and space (Queiroz et al. 2012, Howey et al. 2017), and as this particular diving behaviour primarily occurs during utilization of Gulf Stream waters (Campana et al. 2011), we consider predation by blue shark as unlikely. We therefore concluded that for this predation event, swordfish was the most likely predator, because swordfish consistently perform continuous dives during daylight hours, occasionally disrupted by short lasting basking events (Sepulveda et al. 2010, Dewar et al. 2011).

The observed predation on Atlantic salmon by endothermic fish in the Gulf of St. Lawrence, coincide with the presence of large-sized Atlantic bluefin tuna and porbeagle in these waters during the summer (Hanke et al. 2013, Campana et al. 2015). In a previous study of North American Atlantic salmon tagged with PSATs, predation by lamnid sharks and Atlantic bluefin tuna was spatially segregated (Lacroix 2014). While porbeagle were considered the most likely predators in the Bay of Fundy, predation events occurring on the Scotian Shelf and in proximity to the Cabot Strait were primarily assigned as Atlantic bluefin tuna (Lacroix 2014). In our study, no clear spatial divergence was detected, indicating that predation by Atlantic bluefin tuna and porbeagle may overlapped in the Gulf of St. Lawrence.

For the remaining Atlantic salmon eaten by endothermic fish, the vertical movements recorded by the tags consumed adjacent to the Bay of Biscay and the Irish Shelf resembled a behaviour commonly seen in porbeagle, with a profound diel pattern in depth use, including long-lasting deep dives (Campana et al. 2010, Francis et al. 2015). This suggests predation by porbeagle, which is further strengthened by the spatial-temporal overlap between the predation events and porbeagle's distribution in the northeast Atlantic Ocean (Biais et al. 2017). Alternatively, the shortfin mako (*Isurus oxyrinchus*) may be the culprit, because this endothermic lamnid shark also utilize waters overlapping with the predation events (Compagno 2001). However, as the visceral temperature elevation in shortfin mako does not reach the observed levels in these predation events, or known from species in the genus *Lamna* (Goldman et al. 2004, Sepulveda et al. 2004), porbeagle was considered a more probable predator. For the Atlantic salmon consumed at the Labrador Shelf and in the Irminger Sea, determining the most likely predator was not feasible, as little is known about the distribution and vertical movements of endothermic fish in these waters.

Our results suggest that the overall mortality of adult Atlantic salmon from southern Europe was influenced by their spatial-temporal overlap with porbeagle, and the mortality of adult Atlantic salmon from the Gulf of St. Lawrence was highly affected by their co-occurrence with both porbeagle and Atlantic bluefin tuna. A similar pattern has been recorded in a previous study on marine predation on Atlantic salmon (Lacroix 2014), indicating a particularly high exposure to predation for populations co-occurring with large endothermic fish. In contrast, predation by toothed whales and ectothermic fish is likely to have a lower overall impact on specific populations, due to the lower occurrence and wider distribution of these predation events. However, as predation by toothed whales either occurred along potential migration routes for transatlantic migrants (Bradbury et al. 2016, Gilbey et al. 2017) or in the Labrador

Sea where Atlantic salmon from various origins are known to aggregate (Reddin 2006), toothed whales may contribute to the accumulated mortality for a number of populations.

While the observed predation events on Atlantic salmon explicitly reveal novel ecological interactions, the total mortality imposed on the different groups is perhaps of even greater importance in a management perspective. Despite lack of evidence, it is possible that some of the unknown mortalities were due to predation by pinnipeds, orcas, or other oceanic dolphins, which are unlikely to completely ingest an adult Atlantic salmon either due to gape-size limitations or feeding tactics (Roffe and Mate 1984, Middlemas et al. 2003, Vester and Hammerschmidt 2013). In particular, some of the unknown mortalities observed in coastal areas with dense seal populations were likely a result of seal predation (Ó Cadhla et al. 2007, Hammill et al. 2014b), which has been suggested to have a significant impact on certain populations of Atlantic salmon (Middlemas et al. 2003). The recent recoveries of marine mammals, including seal herds from the Gulf of St. Lawrence, are considered conservational success stories (Hammill et al. 2014b). However, these rehabilitations may impose new challenges when both predator and prey are threatened (Marshall et al. 2016).

In general, Atlantic salmon experience annual mortalities that vary between 70 – 99%, both temporally between years and spatially between rivers (ICES 2017). Most efforts to quantify the ocean mortality of Atlantic salmon have focused on the survival of first time migrants (e.g. Potter et al. 2003, Chaput 2012). However, estimates of adult mortality at sea exist for some populations. Based on post-spawned Atlantic salmon tagged with acoustic tags in the Alta River, a survival corresponding to an instantaneous mortality rate of 1.17 Yr^{-1} was recorded (Hedger et al. 2017b). In a North American river, the decennial instantaneous mortality rates of post spawners ranged from 0.68 – 0.74 Yr^{-1} (Hubley and Gibson 2011). However, in some years

the estimated mortality rate exceeded 5 Yr^{-1}, effectively reflecting an absence of repeat spawners in the reproducing stock (Hubley and Gibson 2011). When comparing our estimates with these studies, it is evident that the total instantaneous mortality rate may have been underestimated for some groups. Compared to other groups, the Atlantic salmon from Norway experienced lower mortality and no confirmed predation. Notably, a greater proportion of tags detaching prematurely for unknown reasons was recorded for the Norwegian populations, and some of these events could have been due to mortality. However, even if every premature detachment was caused by mortality, the total mortality of Norwegian Atlantic salmon would still be lower compared to Atlantic salmon from Canada and southern Europe. This suggest that the observed geographical trend in ocean mortality reflects a variation in mortality regimes imposed on the tagged fish, despite that estimated predation and total mortality rates are somewhat uncertain. To what extent these total mortality rates influence trends in the population abundance is uncertain. However, the spatial pattern present in our data correlates with the ongoing trends in population abundance (ICES 2017), and it is possible that low survival of this life stage may act as an additive stressor to already vulnerable populations.

The use of animal telemetry data for quantifying marine mortality has received increased attention in recent years, particularly with the design of acoustic receiver networks that can provide direct mortality observations in certain systems (Crossin et al. 2017). However, spatially independent information about how, where, and when an individual died while in the open ocean is currently only feasible using PSATs. Despite the increasing evidence of novel interactions between predators and PSAT tagged prey, the use of PSATs for accurately describing mortality, may in some cases be difficult, as tagging effects may distort the estimates (Jepsen et al. 2015). In this study, mortality and predation rates were generally higher for the populations comprising of smaller sized individuals, and our result may be impacted by a

greater physical impediment imposed by the tags on these fish. However, as no size difference was detected regarding the fate of the tagged fish, we argue that the spatial divergence observed in predation and mortality rates is representative of contrasting mortality regimes.

In conclusion, ocean predation and mortality of Atlantic salmon varied largely among geographical areas. Estimated predation and total mortality rates were low for Atlantic salmon from northern Europe, with no confirmed predation of fish originating from Norway. This contrasted the Atlantic salmon from Canada, Spain, and Ireland, where higher predation and total mortality rates were estimated. Predation by Atlantic bluefin tuna primarily occurred in the Gulf of St. Lawrence, while porbeagle predation occurred both in the Gulf of St. Lawrence and in waters from west of the Irish Shelf to the Bay of Biscay. This suggests that predation by Atlantic bluefin tuna and porbeagle is a substantial source of mortality for Atlantic salmon populations co-occurring with these species. Predation by toothed whales and ectothermic fish were less common and occurred over greater geographical areas. The observed predator diversity demonstrated that a variety of large aquatic animals might forage opportunistically on Atlantic salmon during their ocean migration.

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Supplementary material
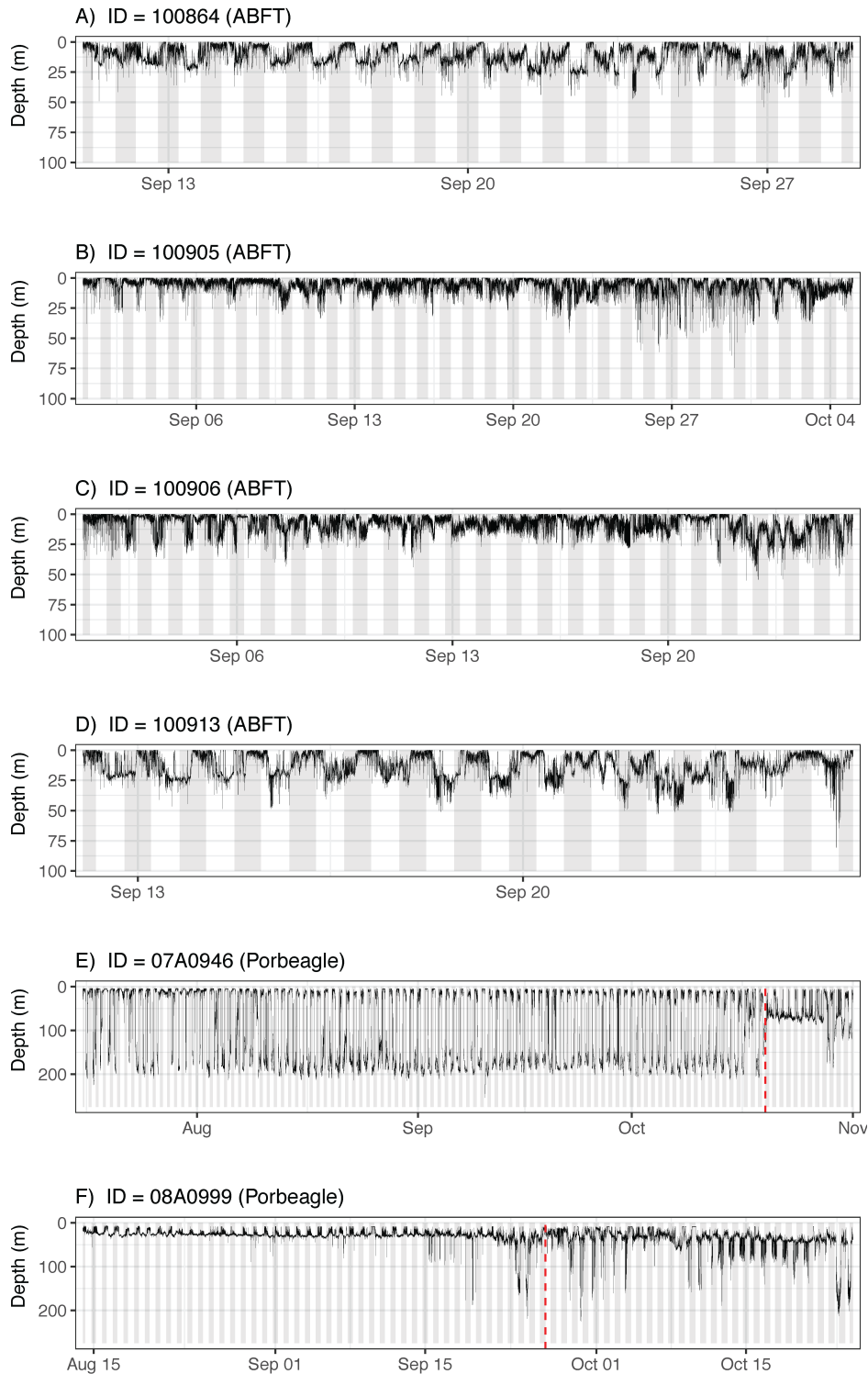
Supplementary figure 1: Vertical profiles of the Atlantic bluefin tuna (ABFT) (A – D) and porbeagle (E – F) tagged in the northwest Atlantic Ocean and uses as references data in the linear discriminant analysis. Tag IDs are stated above plot panels. Shaded areas indicate night. Stippled red vertical lines (E and F) indicate behavioural switches detected by the split-moving window analysis.
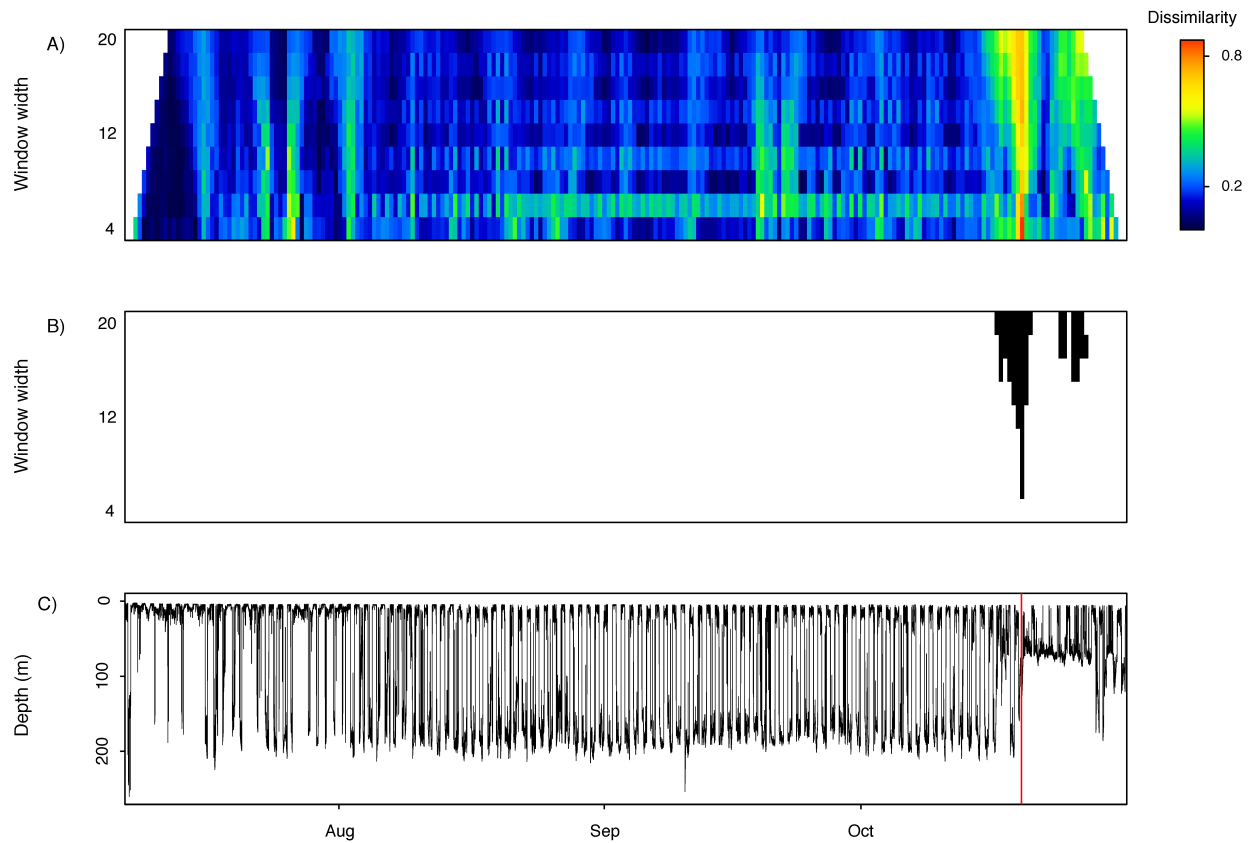
Supplementary figure 2: Example of split-moving window analysis conducted on a porbeagle (ID = 07A0946). A) Dissimilarity between window halves from the split-moving window analysis using different window widths (coded by colour). B) Indicate the significant p-values (black) stacked vertically. C) Depth data used in this analysis, with red vertical line indicating a behavioural switch.
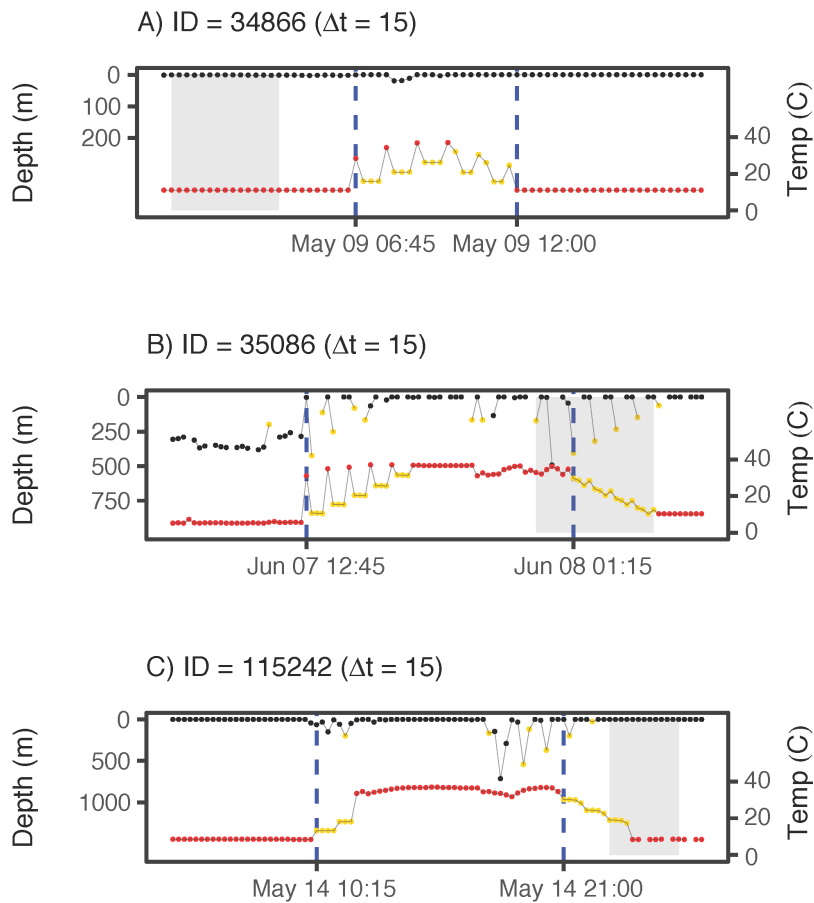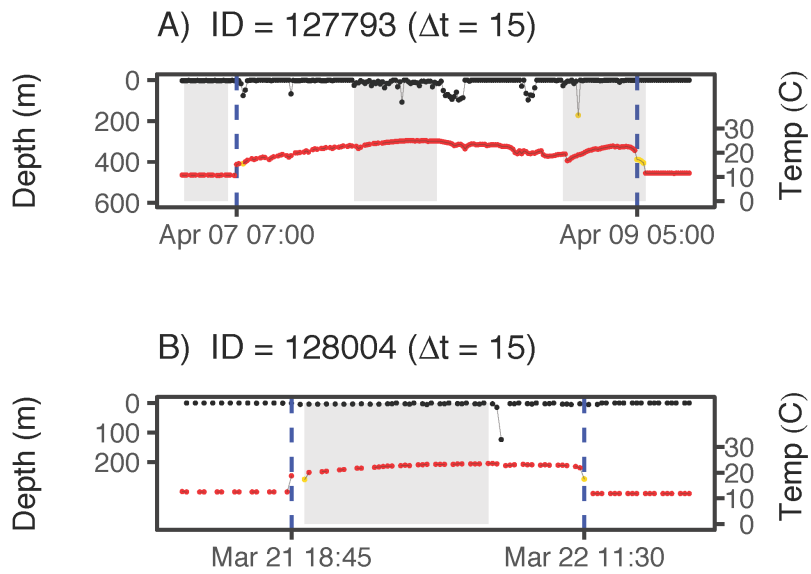
Supplementary figure 3: Depth (black) and temperature (red) profiles for three tags ingested by marine mammals south of Iceland. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion, and shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panels.
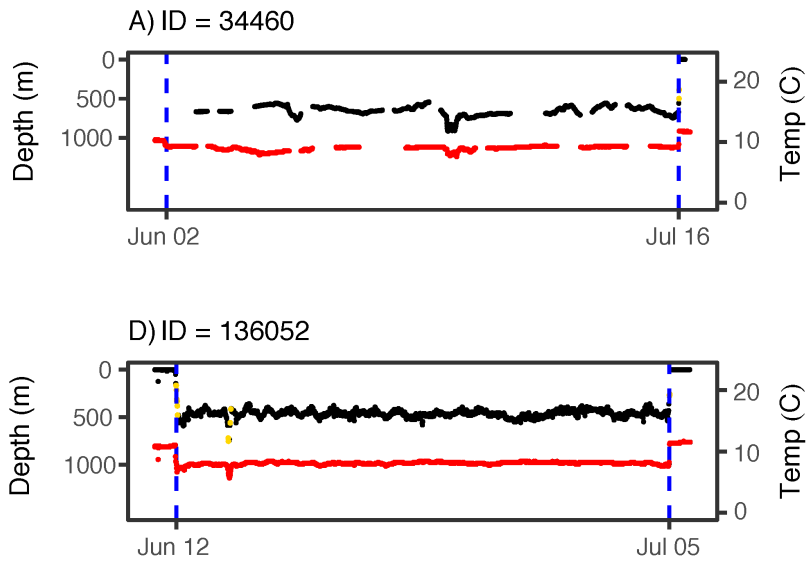
Supplementary figure 4: Depth (black) and temperature (red) profiles for two tags ingested by ectothermic fish south of Iceland. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion. Tag ID is stated above plot panels.
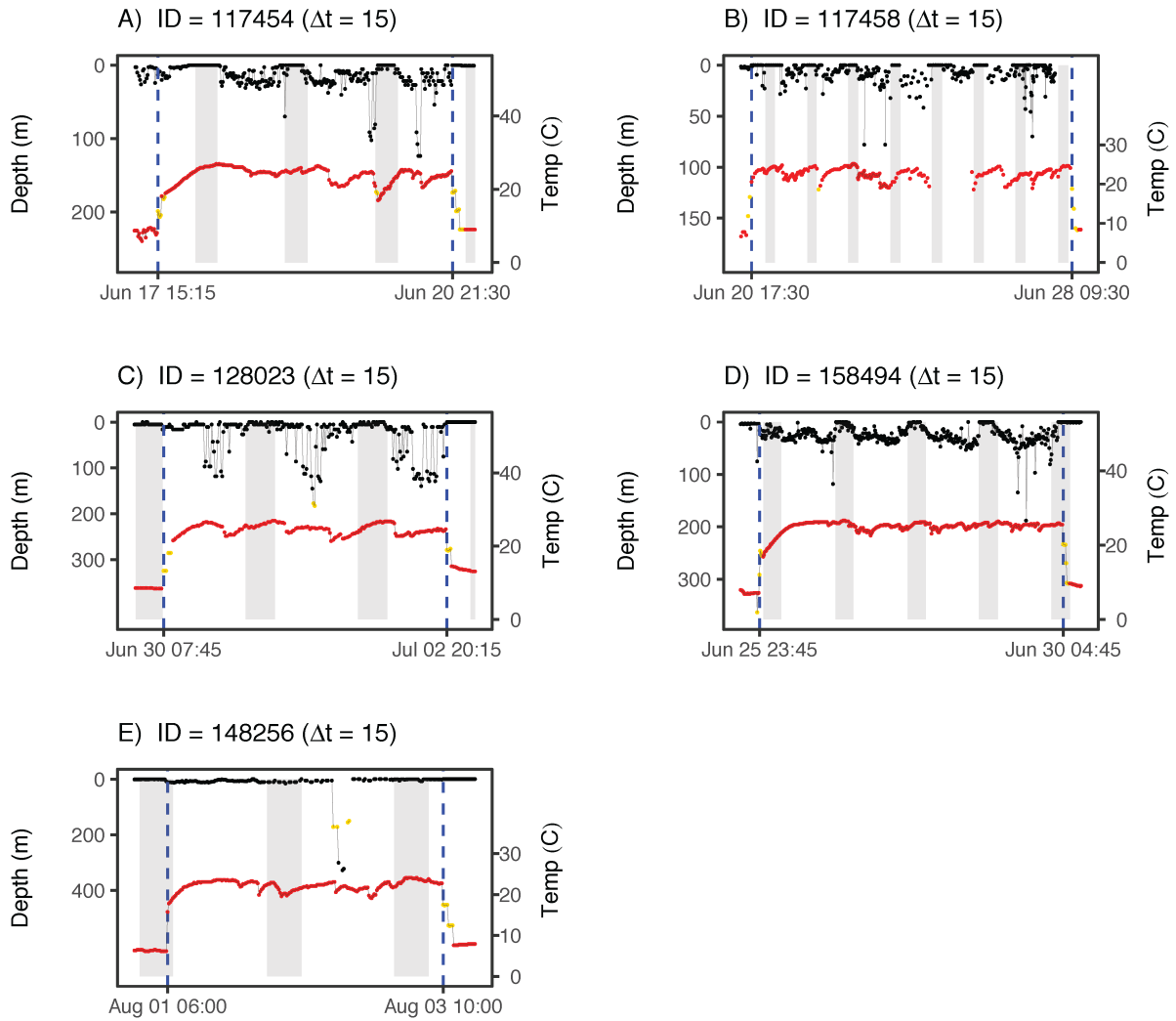
Supplementary figure 5: A – B) Depth (black points) and temperature (red points) profiles for two Atlantic salmon eaten by Atlantic bluefin tuna in the Gulf of St. Lawrence. C – D) Depth (black points) and temperature (red points) profiles for two Atlantic salmon eaten by porbeagle in the Gulf of St. Lawrence. E) Depth (black points) and temperature (red points) profile for an Atlantic salmon eaten by an unknown endothermic fish at the Labrador Shelf. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion, and shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panels.

Supplementary figure 6: A – B) Depth (black points) and temperature (red points) profiles for two Atlantic salmon eaten by endothermic fish in the northeast Atlantic Ocean. Yellow points indicate distorted values (delta-limited values), blue vertical lines indicate time of consumption and expulsion, and shaded regions indicate night. Tag ID and temporal resolution of time series data (Δt) are stated above plot panels.